Nature Conservation

Nature Conservation 57: 89–102 (2024)
DOI: 10.3897/natureconservation.57.107332

Research Article

Traffic mortality of wild forest reindeer *Rangifer tarandus fennicus* in Finland

Milla Niemi[1], Sari C. Cunningham[1], Robert Serrouya[2], Veli-Matti Väänänen[3], Sakari Mykrä-Pohja[4]

1 Metsähallitus, Wildlife Service Finland, Ivalo, Finland
2 Biodiversity Pathways, Kelowna, Canada
3 University of Helsinki, Helsinki, Finland
4 Metsähallitus, Wildlife Service Finland, Pori, Finland
Corresponding author: Milla Niemi (milla.niemi@metsa.fi)

OPEN ACCESS

Academic editor: Ivo Dostál
Received: 31 May 2023
Accepted: 1 January 2024
Published: 16 December 2024

ZooBank: https://zoobank.org/34C1DCD1-CEAF-4879-8CEB-04477A3CE0D2

Citation: Niemi M, Cunningham SC, Serrouya R, Väänänen V-M, Mykrä-Pohja S (2024) Traffic mortality of wild forest reindeer *Rangifer tarandus fennicus* in Finland. In: Papp C-R, Seiler A, Bhardwaj M, François D, Dostál I (Eds) Connecting people, connecting landscapes. Nature Conservation 57: 89–102. https://doi.org/10.3897/natureconservation.57.107332

Abstract

Vehicle collisions kill at least one million ungulates annually in Europe. The number of traffic-killed individuals is usually relatively low for managed species, compared to the annual harvest quota. Therefore, traffic mortality in common ungulate species has historically been seen as a management and traffic safety problem, rather than a conservation issue. However, rare ungulate species, such as European wild forest reindeer (WFR) *Rangifer tarandus fennicus*, challenge this paradigm. The global population of WFR is approximately 5 300 individuals, divided into three main subpopulations: Suomenselkä and Kainuu in Finland, and N-W Russia. WFR females generally produce only one calf per year, which makes this species particularly vulnerable to any additional source of mortality. Here, we investigate traffic mortality of WFR in Finland. For both Finnish WFR subpopulations we estimated a kill rate (the proportion of individuals killed/struck) and, in relation to their winter population sizes, the collision and traffic mortality rates. Our collision data was collected during 2017–2022 by volunteer hunters and consisted of 390 road traffic collisions (407 WFR individuals), with supplementary data on railway collisions. In total, 259 individuals were killed directly in road traffic collisions or euthanized later after tracking (kill rate 64%). An age class (adult/juvenile) was determined for 265 animals (65%), and the results indicated that noticeably more adults than juveniles were killed. In relation to wintering subpopulation sizes, there were higher collision and traffic mortality rates in Suomenselkä (3.0% and 2.0% of the winter population, respectively) than in Kainuu (1.8% and 1.3%). WFR-train collisions occurred in both subpopulations. In Suomenselkä, a railway mortality rate of 0.2% was recorded, while in Kainuu it was 0.7%. We found collision and traffic mortality rates that were relatively low and comparable with those of other ungulate species. However, the relatively high proportion of adults observed among road-killed individuals lends support for further studies to develop species-specific mitigation measures for WFR.

Key words: Collision rate, road-kill, traffic mortality rate, ungulate-vehicle collision

Introduction

It is estimated that almost 30 million mammals are killed on European roads annually (Grilo et al. 2020), with ungulates accounting for at least one million of

those deaths (Langbein et al. 2011). During the last few decades, an increase in certain ungulate populations has led to an increased number of ungulate-vehicle collisions (UVCs) (reviewed by Valente et al. 2020). Most European ungulate species that are recorded in collision statistics are managed by hunting, e.g., wild boar *Sus scrofa* and roe deer *Capreolus capreolus* (Linnell et al. 2020), and the annual number of traffic-killed individuals is usually relatively low when compared to the annual harvest quota (Seiler et al. 2004; Niemi et al. 2015; Neumann et al. 2020). Traffic mortality has therefore primarily been seen as a management and traffic safety issue, especially for species which are overabundant (reviewed by Carpio et al. 2021).

While collisions with common and abundant ungulate species are seen mainly as a traffic safety issue, traffic mortality of some endangered species or isolated populations can reach such high rates as to negatively affect population levels. A well-known example is Florida key deer *Odocoileus virginianus clavium*; approximately half of its documented mortality was due to traffic before mitigation measures were implemented in the riskiest road sections (Lopez et al. 2003; Parker et al. 2011). Dekker (2021) found that traffic mortality could partly explain the decline of elk *Cervus canadensis* and bighorn sheep *Ovis canadensis* populations in Jasper National Park in Alberta, Canada, and Hegel and Russel (2013) suggested that road mortalities could become a future conservation concern for mountain caribou *Rangifer tarandus caribou* in Yukon, Canada.

The persistence of many wild Rangifers is threatened by several anthropogenic factors, such as climate warming, landscape change and traffic-related mortality (Vors and Boyce 2009), and many populations or herds of caribou and reindeer have declined across their range (Gunn et al. 2009). One ungulate species which is potentially negatively affected by traffic mortality is the European wild forest reindeer (or Finnish wild forest reindeer; WFR) *Rangifer tarandus fennicus*, a rare subspecies of the circumpolar reindeer *Rangifer tarandus*. Its conservation status is listed as near threatened, according to the 2019 Red List of Finnish Species (Hyvärinen et al. 2019). Females generally produce only one calf per year, which makes this species particularly vulnerable to any additional source of mortality.

Today, WFR occur only in Finland, and the northwestern parts of Russia, although they previously had a wider distribution. There are currently two distinct subpopulations of WFR in Finland: Kainuu and Suomenselkä. Two decades ago, the size of the Kainuu subpopulation decreased dramatically in just a few years, while the Suomenselkä subpopulation, reintroduced 40 years ago, has increased to approximately 2 000 individuals (Paasivaara et al. 2021). Based on census data from late winter 2023, the current total number of Finnish WFR is about 3 000 individuals (Natural Resources Institute Finland, unpublished data), divided over the two main subpopulations (Fig. 1). In contrast, the Russian WFR population peaked during the 1980s. Since then, the population has decreased from 7 000 to 2 300 individuals (Panchenko et al. 2017; Danilov et al. 2020). Taking both the Finnish and Russian WFR populations into account, the total global population of WFR is approximately 5 300 individuals.

Although the main reasons for WFR population decline in Kainuu and Russia are most likely due to anthropogenic landscape change, increased predation pressure by large carnivores (especially wolves *Canis lupus*, see Kojola et al. 2004, 2009), and to a certain extent poaching (Efimov and Mamontov 2014),

other factors such as traffic related mortality have affected and continue to affect the population persistence of WFR. So far, our knowledge about the survival or mortality patterns of WFR is limited. Pöllänen et al. (2023) showed that the primary cause of mortality of adult GPS-collared WFR females is predation. Accidents and traffic mortality were the second and third most important causes of deaths, and the annual mortality rate from traffic was 0.016 for GPS-collared females in both subpopulations.

As traffic mortality is practically the only direct mortality factor in WFR which can be mitigated, it is important to better understand the magnitude of this problem.

The purpose of our study was to provide basic information about the traffic mortality of WFR in Finland. Specifically, our study aimed to answer the following questions:

1. Is road traffic mortality linked to sex or age class?
2. What percentage of individuals struck in road traffic collisions died?
3. How many road traffic collisions have occurred in relation to subpopulation sizes?
4. What proportion of the two subpopulations have died because of road traffic collisions, and are there differences between the subpopulations?

In addition to road traffic mortality, we calculated the proportion of subpopulations that have died due to railway traffic collisions.

Materials and methods

Study area

We conducted our study in Finland, where two distinct subpopulations of WFR currently exist (Fig. 1, Paasivaara et al. 2021). In addition to these subpopulations, two new subpopulations are being established in western Finland by the ongoing WildForestReindeerLIFE re-introduction project (Metsähallitus, Wildlife Service Finland 2023). These new subpopulations were excluded from this study as there has been no known traffic mortality to date.

The distribution of the Kainuu subpopulation is ca. 15 000 km^2 (in Finland). During winter, WFR gather at lichen eskers found especially in the western parts of this area. In summertime, females in particular are more solitary and widely distributed across the landscape (Natural Resources Institute Finland, unpublished data). The distribution of the Suomenselkä subpopulation is ca. 40 000 km^2. During the last decade, the most important winter pastures have been near Lake Lappajärvi, situated in the south-western part of the distribution area. The summer core area of this subpopulation is in central Finland, but WFR have spread to the northeast towards the reindeer (i.e., domesticated *Rangifer*) herding area.

The density of humans is considerably lower in the Kainuu subpopulation, compared to the Suomenselkä area: 3.1 inhabitants vs. 9.1–14.3 inhabitants per km^2, depending on the province (Statistics Finland 2023). Similarly, the paved road density is lower in the area of the Kainuu subpopulation (0.14 km per km^2) than in the area of the Suomenselkä subpopulation (0.21 km per km^2) (calculated from the data presented in Fig. 2). The railway intersects both areas (Fig. 2).

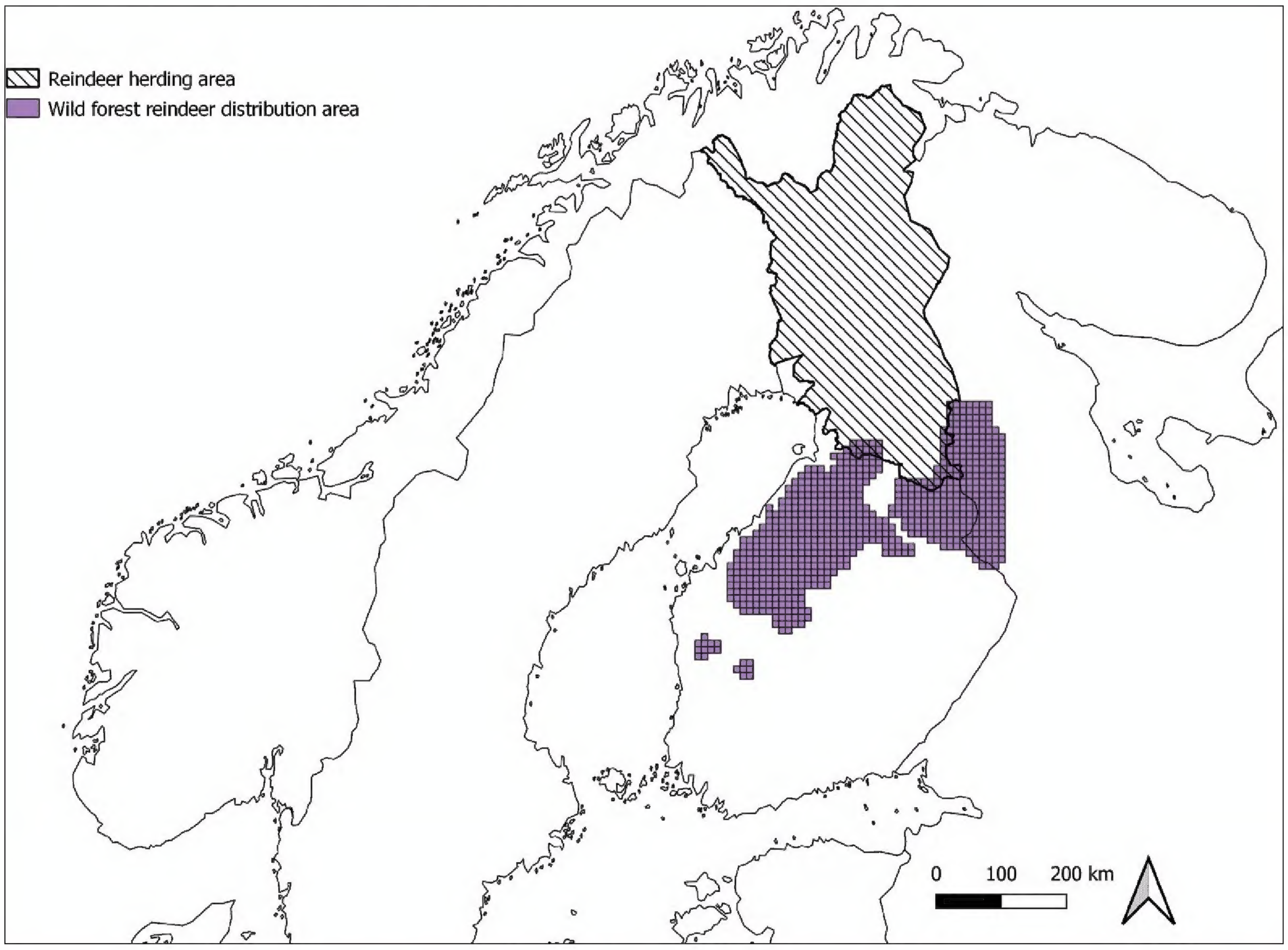

Figure 1. Subpopulations (western Suomenselkä, eastern Kainuu) of wild forest reindeer and reindeer herding area in Finland. Information is provided by Natural Resources Institute Finland (WFR distribution), Reindeer Herders' Association (reindeer herding area) and Eurostat (country borders).

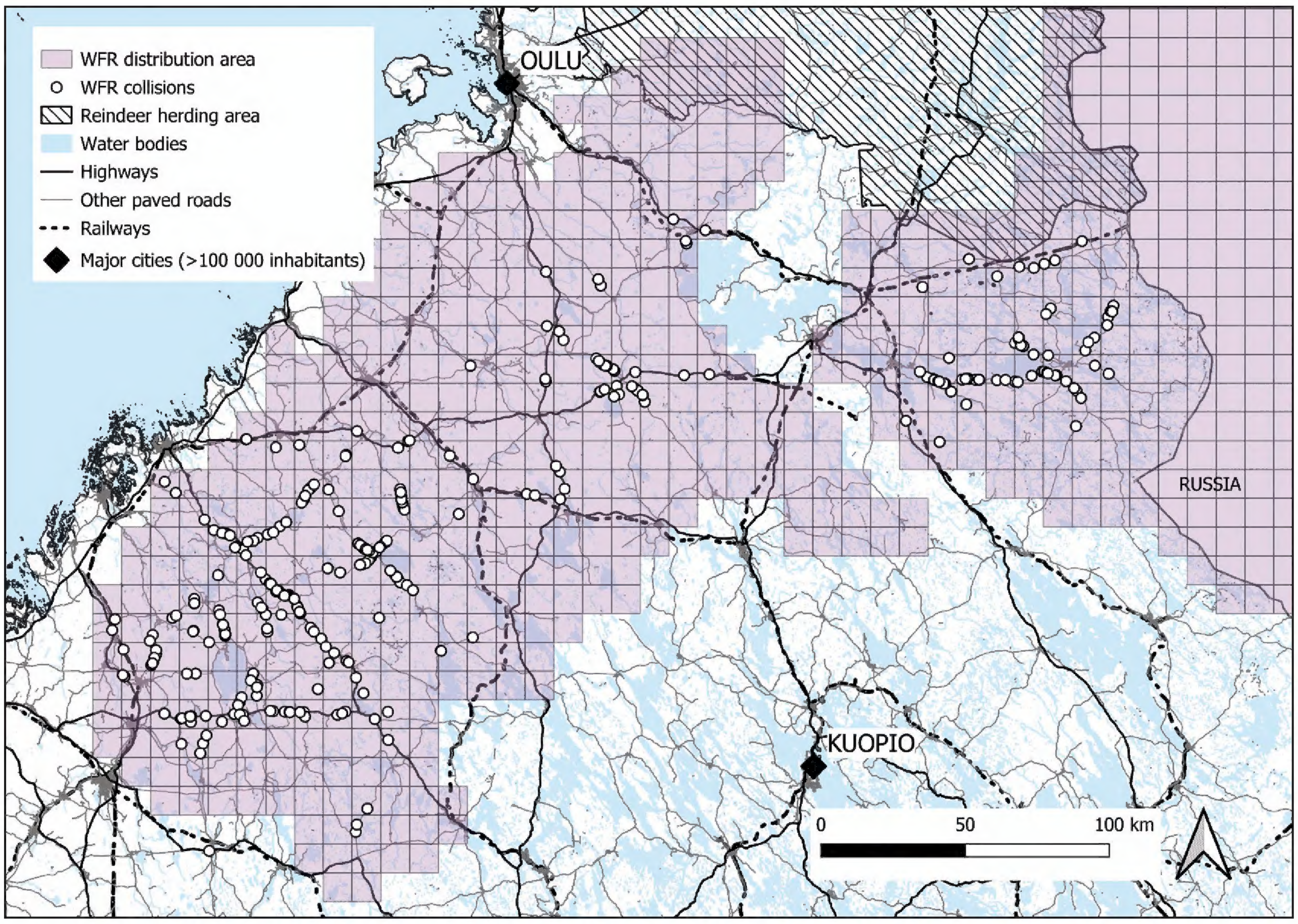

Figure 2. Paved roads, railways and wild forest reindeer -vehicle collisions within the wild forest reindeer distribution area in Finland. Information is provided by the National Land Survey of Finland (roads, railways, waterbodies, cities), Ministry of Agriculture and Forestry of Finland (WFR collisions), Natural Resources Institute Finland (WFR distribution area), Reindeer Herders' Association (reindeer herding area) and Flanders Marine Institute (seas).

Collision data

Drivers are obliged to report all ungulate-vehicle collisions to the emergency number in Finland. This information is forwarded to the Police, who in turn direct trained volunteer local hunters to provide executive assistance. Volunteers check the condition of the struck animal and euthanized it if needed. If the animal has escaped from the collision site, the volunteers attempt to track it to determine if it is injured. In addition to road casualties, volunteers are often asked to remove ungulate carcasses from the railway after collision with a train.

Since the beginning of 2017, volunteers have reported every event they have participated in, by using a mobile or computer application. Volunteers record the species, time, coordinates, and the result of the event (animal was found dead, euthanized, disappeared, not injured). The data collection is coordinated by the Game Management Associations and the database is administered by the Ministry of Agriculture and Forestry of Finland.

Collision data for 2017–2022 was extracted from the register in April 2023. First, we downloaded all collisions that occurred on a road or railway network where the species was identified as WFR. Then, we manually checked the data and excluded events (ten) which were located outside of the current distribution area of WFR (Fig. 1) because it seemed clear that the species was not registered correctly.

Population data

During the last two decades, the wintering populations of WFR have been censused 16 times in Kainuu and eight times in Suomenselkä. Depending on snow conditions, aerial censuses are conducted in late February or early March by the Natural Resources Institute Finland. Censuses are made as a total count, where the aim is to find all individuals (Paasivaara et al. 2021). In 2023, there were approximately 885 WFR in Kainuu (Natural Resources Institute Finland 2023). The latest census of the Suomenselkä subpopulation was made in 2022, when there were almost 2 000 individuals (Table 2; Natural Resources Institute Finland 2023).

For the years when aerial censuses were not conducted (Kainuu in 2018 and 2020; Suomenselkä in 2017, 2019, 2020), the Natural Resources Institute Finland (2023) has provided WFR population size estimates interpolated from the neighboring years' census results.

Data analyses

First, we calculated the percentages of adult individuals and calves in the road collision data and checked whether the sexed individuals were females or males. Then, we calculated a kill rate, a collision rate, and a road mortality rate (see Niemi et al. 2015) for both subpopulations of WFR. The kill rate was calculated from the animals struck, i.e., the percentage of struck animals that died immediately due to the collision or were euthanized afterwards. The collision rate was calculated in relation to population estimates, i.e., how many collisions occur for each 100 individuals assessed in aerial censuses or estimated wintering population (see Table 1). Similarly, the road mortality rate (road-killed individuals for each 100 individuals)

Table 1. The results of the aerial censuses of wild forest reindeer in the Kainuu and Suomenselkä areas, and annual wintering population estimates for the years when aerial censuses were not conducted (*). The information is provided by the Natural Resources Institute Finland (2023).

Subpopulation	2017	2018	2019	2020	2021	2022
Kainuu	749	732*	714	757*	799	829
Suomenselkä	1364*	1431	1610*	1789*	1968	1957

Table 2. Road-killed and struck but escaped WFR in Finland between 2017 and 2022 (total of six years), divided by subpopulations. "Condition unknown" contains individuals that escaped from the collision site and were not found by tracking (121 individuals), where the collision site was not found at all (nine cases) or information was lacking (three cases).

	Road-killed individuals (% of total)	Uninjured individuals	Condition unknown	Total number of individuals struck (% of total)
Suomenselkä	201	11	109	321 (79%)
Kainuu	58	4	24	86 (21%)
In total	259 (64%)	15 (4%)	133 (33%)	407 (100%)

was calculated in relation to aerial census data. Thus, the collision rate was always equal to or higher than the road mortality rate. For the train collision data, we calculated only a railway mortality rate. To simplify the text, we then converted the results to percentages (e.g., a traffic mortality rate of 0.1 = 10%).

We used Fisher's exact test (e.g., Ranta et al. 1999) to test possible differences between subpopulations in collision and mortality rates. Analyses were conducted using R software, version 3.1.3 (R Development Core Team 2015).

Results

A total of 407 WFR were registered as involved in 390 road traffic collisions during the six-year study period (Fig. 2, Table 2). An age class (adult/juvenile) was determined for 265 animals (65%) and the sex (female/male) for 242 animals (59%). There were 100 adult females (25%) and 110 adult males (27%) in the data, respectively. The number of calves was considerably lower; 12 female calves (3%) and 11 male calves (3%) were involved in collisions. In addition, the sex of four calves was not registered.

Altogether, 259 individuals were killed directly in the collisions or euthanized afterwards after tracking (collectively later referred to as road-killed), which yields a kill rate of 64% (Table 2). The condition of 15 individuals (4%) was checked and registered as injured. The rest of the animals, 133 individuals (33%), escaped from the collision sites and/or their condition was unknown.

In relation to wintering population sizes, the Suomenselkä subpopulation had a higher collision rate (3.0%; 3.0 collisions/100 individuals) than the Kainuu subpopulation (1.8%). The difference between subpopulations was statistically significant (DF = 1, $p < 0.001$). Concurrently, the road mortality rate was higher in the Suomenselkä subpopulation (2.0%) than in the Kainuu subpopulation (1.3%). A statistically significant difference was observed between subpopulations (DF = 1, $p = 0.003$).

WFR-train collisions occurred in both subpopulations. The total number of registered collisions was 19 in Kainuu and eight in Suomenselkä. At least 30 individuals died in these collisions in Kainuu, giving a railway mortality rate of 0.7%. In Suomenselkä, 22 individuals were reported to die in train collisions (a railway mortality rate of 0.2%).

Discussion

In this study, we gathered basic information about traffic mortality of WFR. When looking at the demographical status of road-killed individuals, the percentage of road-killed calves (those classified as juveniles) was less than five percent. This percentage was lower than the percentage of calves in the population; for example, in the aerial census conducted in April 2021, the percentage of calves was 14.0% in Kainuu and 13.5% in the Suomenselkä subpopulation (Paasivaara et al. 2021). Our dataset was too small to draw any firm conclusions, but the results suggest that the road mortality of WFR might be adult biased. If this is correct, the possible effect of road mortality on population persistence could be larger than the collision numbers indicate. Adult females in particular are critical to ungulate population growth and survival (Gaillard et al. 1998).

Traffic mortality, unlike predation-related mortality, does not appear to be linked to an animal's physical condition, at least in some circumstances. Gunson et al. (2022) found that road-killed elk were in better physical condition compared to individuals killed by predators, and therefore suggested that vehicle collisions are an additive source of mortality. Although our data did not detail the physical condition or accurate age structure of road-killed WFR, a study by Karhula (2021) found that adult road-killed WFR were younger than individuals killed by predators. This indicates that the expected contribution of road-killed WFR to the population growth will be missed.

Our finding that there were almost an equal number of adult females and males in the collision data was somewhat surprising. There are slightly more females than males in the WFR population (Natural Resources Institute Finland, unpublished data), but the ratio of close to 1:1 was still unexpected. Ungulate males are often over-represented in collision statistics in relation to the demographic population structure (Etter et al. 2002; Lopez et al. 2003; Olson et al. 2014; Gunson et al. 2022; but see Madsen et al. 2002), which is probably at least partly due to their longer daily movements, especially during the rut (Webb et al. 2010; Niemi et al. 2013). One possible explanation for our results could be the strong herding behavior in WFR, especially in winter, which could lead to both sexes crossing roads in equal numbers. Our observation underlines again the relative importance of traffic mortality for the WFR population; it seems that the most valuable individuals for the population (adult females) are also relatively vulnerable to traffic mortality.

We found a kill-rate of 64%, i.e., approximately six out of ten WFR struck died due to road traffic collisions. This is a much lower rate than reported in earlier UVC-studies; for example, Almkvist et al. (1980) found a kill-rate of 94% for roe deer and > 80% for moose *Alces alces*. However, only 4% of struck WFR were classified as uninjured in our data, which means that approximately one third of hit individuals disappeared after the collision. It is not known what proportion of these animals were fatally wounded and would have died later. It could be

speculated that the percentage might be high; WFR tend to move and cross roads as a herd especially in wintertime, and tracking an injured individual among others can be impossible. In addition, not all accidents are reported to start with (Bíl and Andrášik 2020). We therefore note that even though the kill-rate we found was relatively low, the true number of individuals which are killed in road traffic is probably more or less the same as the number of collisions. Thus, if we want to evaluate the proportion of road killed individuals in WFR populations, reporting a collision rate might be a better indicator.

When looking at the subpopulation level, the collision rate in relation to the wintering population size was higher in the Suomenselkä subpopulation than in Kainuu (3.0% vs. 1.8%). This was true also for road mortality rates (2.0% vs. 1.3%). The observed proportions were approximately the same as those reported elsewhere for other ungulate species. Seiler et al. (2004) estimated that 4% of the Swedish moose population was killed in road traffic. In a study conducted in a densely populated area in southern Finland, Niemi et al. (2015) reported road traffic mortality rates ranging from 2.1% to 6.5% of the wintering population, depending on the ungulate species. The most likely factor explaining the observed differences between WFR subpopulations is traffic volume, which is known to affect the number of ungulate-vehicle collisions (Seiler 2004; Bíl et al. 2021). There are more major roads in the distribution area of the Suomenselkä subpopulation than in Kainuu, and WFR in Suomenselkä are therefore more likely to cross roads during their daily routines and seasonal movements.

Even though our study was based on only six years of data, the high proportion of adult road-killed WFR implies that traffic mortality should be seriously considered as a conservation issue. This calls for species-specific mitigation measures for WFR, which differs from other wild ungulates as a strongly migratory, herding species. While widely used methods such as under and overpasses with wildlife fences (Clevenger 2005; Olsson and Widen 2008; Huijser et al. 2016) are not cost-effective mitigation measures for WFR moving long distances and crossing some (non-fenced minor) roads maybe only twice per year (but see Sawyer et al. 2012, 2016), identifying high risk road sections might be a key to target other measures such as wildlife detection systems and short-term temporal warning signs (Huijser et al. 2015). In the future, intelligent systems incorporating sensor technologies and machine learning (reviewed by Nandutu et al. 2022) will be increasingly used to detect road-crossing animals, including WFR, to give drivers more time to react.

In this study, we concentrated mainly on road-traffic mortality of WFR because the volunteer-based UVC-data collection system used in Finland is inadequate for collecting a comprehensive dataset from railroads. However, as our limited data showed, WFR are occasionally also killed in train collisions, sometimes several individuals at one time. Rolandsen et al. (2015) highlight the importance of similar factors affecting both road and railway collisions, such as animal population density, and traffic intensity. For semi-domesticated reindeer, they found a positive correlation between the frequency of collisions and reindeer density, but only in areas where the railway crossed the winter range. Understanding the factors that contribute towards WFR railway mortality will allow us to develop mitigation measures for railway systems as well. As with the road network, the first step will be to recognize

collision hotspots and then apply mitigation measures such as thermal cameras and early acoustic warning (Bhardwaj et al. 2022) to reduce the risk of WFR-train collisions.

Our study provides only the very first information about traffic mortality of WFR. The dataset we used should be better utilized in the future, for example to recognize spatial collision hotspots (Shilling and Waetjen 2015; Bíl et al. 2019), and again highlight the areas with high risk of WFR collisions (e.g., Morelle et al. 2013). By combining the collision data with different landscape and forest structure datasets, we could study how landscape and habitat variables affect the location of collisions (Danks and Porter 2010; Galinskaitė et al. 2022) and try to predict future collision hotspots based on the environmental and road-related variables (Laube et al. 2023). Also, the existing collision data provides an opportunity to study seasonal patterns of WFR collisions in a more detailed way.

We were only able to use WFR collision data in this study. In the future, it would be useful to use collision data together with GPS data from satellite-collared WFR. This would help us identify areas where animals are more likely to cross the main roads during their annual movements. It is noteworthy that the potential crossing sites or areas are not necessarily the same as indicated by the animal-vehicle collision data (Neumann et al. 2012; Lee et al. 2023), which shows that collision data alone does not provide us with a complete understanding. In addition, GPS-data would help us to recognize the effects of roads and traffic on individual movements (see Wilson et al. 2016), to better understand how anthropogenic factors affect the behavior and survival of WFR.

Conclusions

Here, we studied traffic mortality of wild forest reindeer in Finland by using collision data which was collected during 2017–2022 by volunteer hunters. Our results indicate an adult bias in road mortality. Interestingly, adult females and males were almost equally represented in the collision data, unlike other ungulate traffic mortality studies where males are often over-represented. We have suggested that this may be due to the strong herding behavior exhibited in WFR, especially in winter. Although our dataset was limited, these results cumulatively suggest the relative importance of traffic mortality for WFR population persistence. In particular, the most valuable individuals for the population, adult females, appear to be relatively vulnerable to traffic mortality. Future studies may further use this dataset to focus on seasonal patterns of WFR collisions in a more detailed manner and predict collision hotspots. Such studies could help to plan and locate species-specific mitigation measures to reduce traffic mortality of this endemic ungulate species.

Acknowledgements

We highly appreciated the opportunity to use the ungulate-vehicle collision data conducted by voluntary hunters and managed by Game Management Associations. Three anonymous referees provided helpful comments that improved our manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was part of the EU-funded project WildForestReindeerLIFE (LIFE15 NAT/FI/000881). Project beneficiaries take full responsibility for the materials included in this publication. Texts and pictures published in this article should not be interpreted to represent the official views or standpoints of the European Commission or the European Union.

Author contributions

Milla Niemi conceived the study, performed the data analysis, took the lead in writing the manuscript with support from Sari C. Cunningham and Robert Serrouya, and designed the figures. All authors read and revised the manuscript, and approved the submitted version.

Author ORCIDs

Milla Niemi https://orcid.org/0000-0002-1711-8692
Sari C. Cunningham https://orcid.org/0009-0001-0308-1593
Robert Serrouya https://orcid.org/0000-0001-5233-6081
Sakari Mykrä-Pohja https://orcid.org/0000-0002-9434-1265

Data availability

All of the data that support the findings of this study are available in the main text.

References

Almkvist B, André T, Ekblom S, Rempler SA (1980) Slutrapport Viltolycksprojekt. Final Report of the Game Accident Project. Swedish National Road Administration, Borlänge, Sweden, TU146: 1980–05, 117 pp. [In Swedish with an English summary] http://www.algen.se/assets/doclib/1/viltolycksprojektet-viol-slutrapport.pdf

Bhardwaj M, Olsson M, Håkansson E, Söderström P, Seiler A (2022) Ungulates and trains – Factors influencing flight responses and detectability. Journal of Environmental Management 313: e114992. https://doi.org/10.1016/j.jenvman.2022.114992

Bíl M, Andrášik R (2020) The effect of wildlife carcass underreporting on KDE+ hotspots identification and importance. Journal of Environmental Management 275: e111254. https://doi.org/10.1016/j.jenvman.2020.111254

Bíl M, Andrášik R, Sedoník J (2019) A detailed spatiotemporal analysis of traffic crash hotspots. Applied Geography 107(41): 82–90. https://doi.org/10.1016/j.apgeog.2019.04.008

Bíl M, Andrášik R, Cícha V, Arnon A, Kruuse M, Langbein J, Náhlik A, Niemi M, Pokorny B, Colino-Rabanal VJ, Rolandsen CM, Seiler A (2021) COVID-19 related travel restrictions prevented numerous wildlife deaths on roads: A comparative analysis of results from 11 countries. Biological Conservation 256: e109076. https://doi.org/10.1016/j.biocon.2021.109076

Carpio AJ, Apollonio M, Acevedo P (2021) Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. Mammal Review 51(1): 95–108. https://doi.org/10.1111/mam.12221

Clevenger AP (2005) Conservation value of wildlife crossings: Measures of performance and research directions. GAIA – Ecological Perspectives for Science and Society 14(2): 124–129. https://doi.org/10.14512/gaia.14.2.12

Danilov PI, Panchenko DV, Tirronen KF (2020) Severniy Olen Vostochnoy Fennoskandiy [Северный Олень Восточной Фенноскандии] (Reindeer of the Eastern Fennoscandia). KarRC RAS, Petrozavodsk, 187 pp. [In Russian]

Danks ZD, Porter WF (2010) Temporal, spatial, and Landscape habitat characteristics of moose-vehicle collisions in Western Maine. The Journal of Wildlife Management 74(6): 1229–1241. https://doi.org/10.1111/j.1937-2817.2010.tb01243.x

Dekker D (2021) Road and rail fatalities of elk, bighorn sheep, and gray wolves in Jasper National Park, Alberta, 1980–2018. Northwestern Naturalist (Olympia, Wash.) 102(1): 83–88. https://doi.org/10.1898/1051-1733-102.1.83

Efimov VA, Mamontov VN (2014) Monitoring dikogo severnogo olenya (*Rangifer tarandus* L.) taegnoy zoni arhaneglskoy oblasti [Мониторинг дикого северного оленя (*Rangifer tarandus* L.) таёжной зоны архангельской области] (Wild reindeer monitoring in the taiga zone of the Arkhangelsk Region). Vestnik ohotovedeniya 11: 166–170.

Etter DR, Hollis KM, Van Deelen TR, Ludwig DR, Chelsvig JE, Anchor CL, Warner RE (2002) Survival and movements of white-tailed deer in suburban Chicago, Illinois. The Journal of Wildlife Management 66(2): 500–510. https://doi.org/10.2307/3803183

Flanders Marine Institute (2021) Global Oceans and Seas, version 1. https://doi.org/10.14284/542

Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology & Evolution 13(2): 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Galinskaitė L, Ulevičius A, Valskys V, Samas A, Busher PE, Ignatavičius G (2022) The influence of landscape structure on wildlife–vehicle collisions: Geostatistical analysis on hot spot and habitat proximity relations. ISPRS International Journal of Geo-Information 11(1): e63. https://doi.org/10.3390/ijgi11010063

Grilo C, Koroleva E, Andrášik R, Bíl M, Gonzalez-Suarez M (2020) Roadkill risk and population vulnerability in European birds and mammals. Frontiers in Ecology and the Environment 18(6): 323–328. https://doi.org/10.1002/fee.2216

Gunn A, Russell D, White RG, Kofinas G (2009) Facing a Future of Change: Wild Migratory Caribou and Reindeer. Arctic 62(3): 3–6. http://www.jstor.org/stable/40513303

Gunson KE, Clevenger AP, Ford AT (2022) A comparison of elk-vehicle collision patterns with demographic and abundance data in the Central Canadian Rocky Mountains. Conservation Science and Practice 4(12): e12842. https://doi.org/10.1111/csp2.12842

Hegel TM, Russel K (2013) Status of northern mountain caribou (*Rangifer tarandus caribou*) in Yukon, Canada. Rangifer 33(2): 59–70. https://doi.org/10.7557/2.33.2.2528

Huijser MP, Mosler-Berger C, Olsson M, Strein M (2015) Wildlife warning signs and animal detection systems aimed at reducing wildlife-vehicle collisions. In: Van der Ree R, Grilo C, Smith D (Eds) Ecology of Roads: A Practitioner's Guide to Impacts and Mitigation. John Wiley & Sons Ltd., Chichester, 198–212. https://doi.org/10.1002/9781118568170.ch24

Huijser MP, Fairbank ER, Camel-Means W, Graham J, Watson V, Basting P, Becker D (2016) Effectiveness of short sections of wildlife fencing and crossing structures

along highways in reducing wildlife–vehicle collisions and providing safe crossing opportunities for large mammals. Biological Conservation 197: 61–68. https://doi.org/10.1016/j.biocon.2016.02.002

Hyvärinen E, Juslén A, Kemppainen E, Uddström A, Liukko U-M [Eds] (2019) The 2019 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus. Helsinki, 704 pp. http://hdl.handle.net/10138/299501

Karhula K (2021) Liikenteen ja suurpetojen tappamien metsäpeurojen ikäjakaumat. Master's thesis, University of Helsinki. https://urn.fi/URN:NBN:fi:hulib-202103031597 [In Finnish]

Kojola I, Huitu O, Toppinen K, Heikura K, Heikkinen S, Ronkainen S (2004) Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. Journal of Zoology 263(3): 229–235. https://doi.org/10.1017/S0952836904005084

Kojola I, Tuomivaara J, Heikkinen S, Heikura K, Kilpeläinen K, Keränen J, Paasivaara A, Ruusila V (2009) European wild forest reindeer and wolves: Endangered prey and predators. Annales Zoologici Fennici 46(6): 416–422. http://www.sekj.org/PDF/anzf46/anzf46-416.pdf

Langbein J, Putman R, Pokorny B (2011) Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. In: Putman R, Apollonio M, Andersen R (Eds) Ungulate Management in Europe: Problems and Practices. Cambridge University Press, UK, 215–259. https://doi.org/10.1017/CBO9780511974137.009

Laube P, Ratnaweera N, Wróbel A, Kaelin I, Stephani A, Reifler-Baechtiger M, Graf RF, Suter S (2023) Analysing and predicting wildlife–vehicle collision hotspots for the Swiss road network. Landscape Ecology 38(7): 1765–1783. https://doi.org/10.1007/s10980-023-01655-5

Lee TS, Jones PF, Jakes AF, Jensen M, Sanderson K, Duke D (2023) Where to invest in road mitigation? A comparison of multiscale wildlife data to inform roadway prioritization. Journal for Nature Conservation 71: e126327. https://doi.org/10.1016/j.jnc.2022.126327

Linnell JDC, Cretois B, Nilsen EB, Rolandsen CM, Solberg EJ, Veiberg V, Kaczensky P, Van Moorter B, Panzacchi M, Rauset GR, Kaltenborn B (2020) The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. Biological Conservation 244: e108500. https://doi.org/10.1016/j.biocon.2020.108500

Lopez RR, Vieira MEP, Silvy NJ, Frank PA, Whisenant SW, Jones DA (2003) Survival, mortality, and life expectancy of Florida Key deer. The Journal of Wildlife Management 67(1): 34–45. https://doi.org/10.2307/3803059

Madsen AB, Strandgaard H, Prang A (2002) Factors causing traffic killings of roe deer *Capreolus capreolus* in Denmark. Wildlife Biology 8(1): 55–61. https://doi.org/10.2981/wlb.2002.008

Metsähallitus, Wildlife Service Finland (2023) Metsähallitus, Wildlife Service Finland. https://www.metsa.fi/projekti/metsapeuralife/palautusistutukset-etelaisella-suomenselalla/

Morelle K, Lehaire F, Lejeune P (2013) Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. Nature Conservation 5: 53–73. https://doi.org/10.3897/natureconservation.5.4634

Nandutu I, Atemkeng M, Okouma P (2022) Intelligent systems using sensors and/or machine learning to mitigate wildlife–vehicle collisions: A review, challenges, and new perspectives. Sensors 22(7): e2478. https://doi.org/10.3390/s22072478

Natural Resources Institute Finland (2023) Natural Resources Institute Finland. https://www.luke.fi/fi/seurannat/kainuun-metsapeurakanta-edelleen-lievassa-kasvussa [In Finnish]

Neumann W, Ericsson G, Dettki H, Bunnefeld N, Keuler NS, Helmers DP, Radeloff VC (2012) Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. Biological Conservation 145(1): 70–78. https://doi.org/10.1016/j.biocon.2011.10.011

Neumann W, Widemo F, Singh NJ, Seiler A, Cromsigt JPGM (2020) Strength of correlation between wildlife collision data and hunting bags varies among ungulate species and with management scale. European Journal of Wildlife Research 66: e86. https://doi.org/10.1007/s10344-020-01421-x

Niemi M, Melin M, Matala J, Häggblom K, Hokkanen P, Tiilikainen R, Paasivaara A, Pusenius J, Järvenpää H (2013) Peuroja vai kauriita – mitä peurakolaritilastot sisältävät? Suomen Riista 59: 100–113. http://urn.fi/URN:NBN:fi-fe201702211832 [In Finnish with English summary]

Niemi M, Matala J, Melin M, Eronen V, Järvenpää H (2015) Traffic mortality of four ungulate species in southern Finland. Nature Conservation 11: 13–28. https://doi.org/10.3897/natureconservation.11.4416

Olson DD, Bissonette JA, Cramer PC, Bunnel KD, Coster DC, Jackson PJ (2014) Vehicle collisions cause differential age and sex-specific mortality in mule deer. Advances in Ecology. https://doi.org/10.1155/2014/971809 [Article ID971809]

Olsson MPO, Widen P (2008) Effects of highway fencing and wildlife crossings on moose *Alces alces* movements and space use in southwestern Sweden. Wildlife Biology 14(1): 111–117. https://doi.org/10.2981/0909-6396(2008)14[111:EOHFAW]2.0.CO;2

Paasivaara A, Hyvärinen M, Timonen P, Luoma M, Niemi M (2021) Metsäpeurakanta kasvussa. Metsästäjä 3/2021: 42–43. [In Finnish]

Panchenko DV, Tirronen KF, Danilov PI, Bljudnik LV, Miettunen J, Belkin VV, Simonov SA (2017) Otsenka chislenosti i razpredelenie lesnogo severnogo olenya (*Rangifer tarandus fennicus* Lönnb.) v Kareliy [Оценка численности и распределение лесного северного оленя (*Rangifer tarandus fennicus* Lönnb.) в Карелии] (Assessment of the forest reindeer (*Rangifer tarandus fennicus* Lönnb.) number and distribution in the Republic of Karelia). Vestnik ohotovedeniya 14(3): 156–163.

Parker ID, Lopez RR, Silvy NJ, Davis DS, Owen CB (2011) Long-term effectiveness of US 1crossing project in reducing Florida Key deer mortality. Wildlife Society Bulletin 35(3): 296–302. https://doi.org/10.1002/wsb.45

Pöllänen AT, Pakanen V-M, Paasivaara A (2023) Survival and cause-specific mortality in adult females of a northern migratory ungulate. European Journal of Wildlife Research 69(3): e60. https://doi.org/10.1007/s10344-023-01686-y

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://R-project.org/

Ranta E, Rita H, Kouki J (1999) Biometria. Tilastotiedettä ekologeille. Helsinki University Press, Helsinki, 596 pp.

Rolandsen CM, Solberg EJ, Van Moorter B, Strand O (2015) Dyrepåkjørsler på jernbanen i Norge 1991–2014. (Animal-Train accidents on the railway in Norway 1991–2014). NINA Rapport 1145: e111. [In Norwegian with an English summary]

Sawyer H, Lebeau C, Hart T (2012) Mitigating roadway impacts to migratory mule deer – A case study with underpasses and continuous fencing. Wildlife Society Bulletin 36(3): 492–498. https://doi.org/10.1002/wsb.166

Sawyer H, Rodgers PA, Hart T (2016) Pronghorn and mule deer use of underpasses and overpasses along U.S. Highway 191. Wildlife Society Bulletin 40(2): 211–216. https://doi.org/10.1002/wsb.650

Seiler A (2004) Trends and spatial patterns in ungulate-vehicle collisions in Sweden. Wildlife Biology 10(4): 301–313. https://doi.org/10.2981/wlb.2004.036

Seiler A, Helldin J-O, Seiler C (2004) Road mortality in Swedish mammals: Results of a drivers' questionnaire. Wildlife Biology 10(3): 225–233. https://doi.org/10.2981/wlb.2004.028

Shilling FM, Waetjen DP (2015) Wildlife-vehicle collision hotspots at US highway extents: scale ad data source effects. In: Seiler A, Helldin J-O (Eds) Proceedings of IENE 2014 International Conference on Ecology and Transportation, Malmö, Sweden. Nature Conservation 11: 41–60. https://doi.org/10.3897/natureconservation.11.4438

Statistics Finland (2023) Statistics Finland. https://stat.fi/tup/tilastotietokannat/index_en.html

Valente AM, Acevedo P, Figueiredo AM, Fonseca C, Torres RT (2020) Overabundant wild ungulate populations in Europe: Management with consideration of socio-ecological consequences. Mammal Review 50(4): 353–366. https://doi.org/10.1111/mam.12202

Vors LS, Boyce MS (2009) Global declines of caribou and reindeer. Global Change Biology 15(11): 2626–2633. https://doi.org/10.1111/j.1365-2486.2009.01974.x

Webb SL, Gee KL, Strickland BK, Demarais S, DeYoung RW (2010) Measuring fine-scale white-tailed deer movements and environmental influences using GPS collars. International Journal of Ecology. International Journal of Ecology 459610: 1–12. https://doi.org/10.1155/2010/459610

Wilson RR, Parrett LS, Joly K, Dau JR (2016) Effects of roads on individual caribou movements during migration. Biological Conservation 195: 2–8. https://doi.org/10.1016/j.biocon.2015.12.035